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Spirodela oligorrhiza collected in Missouri

ALBERT SAEGER[1]

(WITH PLATE 13)

A species of Lemnaceae, *Spirodela oligorrhiza* (Kurz) Hegelm., not previously reported from North America, was collected by the writer in one of the slow-flowing streams in a wooded section of Swope Park, Kansas City, Missouri (U. S. A.), on Nov. 2, 1930. A portion of the stream which had been dammed by a fallen log was covered with thousands of specimens. *S. polyrrhiza* (L.) Schleid. was also present in small numbers. The two species could be distinguished easily by differences in size, shape, venation, and number of roots per plant. The identification was made from the description in Hegelmaier's monograph (1868, revised 1895). No other species of the genus other than the common *S. polyrrhiza* has to the writer's knowledge been described from North America. Palisot (1816) mentions *S. thermalis* from Virginia, but Schleiden (Hegelmaier 1868, p. 156) found it to be *S. polyrrhiza*. Bravo (1930) reports only *S. polyrrhiza* from Mexico. Hegelmaier (1878) states that only *S. polyrrhiza* is indigenous in Brazil. Thompson describes a second species of the genus for South America, *S. punctata* (Meyer) Thompson, based upon specimens in the United States National Herbarium which were collected in 1839 at Orange Harbor, Tierra del Fuego. His description and the accompanying figure do not correspond with the plants collected in Missouri. Recently Koch (1932) described a new species of Spirodela from Montevideo, Uruguay, *S. intermedia* W. Koch, which differs from both *S. polyrrhiza* and *S. oligorrhiza*, especially in the position of the roots (up to 18 in number) with respect to the basal bract.

Some of the specimens collected were pressed for the herbarium, and others were maintained in an aquarium for further study. Since the identification of certain Lemnaceae in the vegetative state is very difficult and uncertain on account of the extreme variation resulting from differences in environment, it has become my practice to cultivate newly collected specimens of doubtful identity in a synthetic nutrient solution (Saeger, 1925, 1933). In this way the development of vegetative characters in the different species is conditioned by an environment initially the same for all species under examination. Cultures of eleven species have been maintained for comparative study: two of *Spirodela*, six of *Lemna*, and three of

[1] Fellow in the Biological Sciences, National Research Council.

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Wolffia. In this group *S.oligorrhiza* may be identified readily, even in the vegetative state.

Hegelmaier reported *S. oligorrhiza* from Australia, India, Java, and Japan. Recently Lancaster (1930) reported it from New Zealand. It is not likely that this species has been overlooked in the past by botanists in this country. It may have been introduced recently. It was again collected by Dr. F. H. Woods in September, 1932, in southwest Missouri, from a pond containing goldfish. Inquiry revealed that the plants in this pond had been obtained from a supply house in Ohio, but no information could be obtained about the original source of the plants. No doubt *S. oligorrhiza* has become established in other localities and will be found by other collectors. It is one of five species I used in a study of the relation of manganese to nutrition. A photograph of this species may be found in this publication (Saeger, 1933, plate 9). This species has produced flowers on several occasions while growing in pure culture.[2] Since flowering of the Lemnaceae is of special interest (Saeger, 1929; Hicks, 1932), the conditions which induced this flowering are being studied.

A brief description of the species is given, so that others who collect similar specimens may readily identify it. Hegelmaier's excellent monograph (1868, rev. 1895) should, however, be consulted for additional information.

Spirodela oligorrhiza (*Kurz*) *Hegelm.*

Plants oblong-obovate, strongly asymmetric, base bluntly cuneate, apex obtusely pointed, united into colonies of from 2 to 10. Plants 4 mm. long $\times$2.6 mm. wide or smaller, their size varying with growth conditions. A nodal embryonic point occurs about one third the distance from base to apex, from which arise 2 to 6 adventitious roots, 5 to 6 veins, and 2 vegetative points. Buds develop from these vegetative points to form the daughter plants. A basal stalk connects the daughter plant with its parent. In very young plants a basal bract occurs, divided into a dorsal and a ventral portion, the latter extending over the node, and later being punctured by all the outgrowing roots. This structure becomes almost obliterated when the plants have reached maturity. (It is not found in any species of Lemna, but a similar bract occurs in *S. polyrrhiza*.) Roots 3 cm. long or shorter, with sharp-pointed root cap. A row of papules prominent on upper surface along midvein. A sac-like spathe encloses two stamens and one pistil. Stamens about 1 mm. long, the one nearest the base ripening a day before the second one. Anthers 2, transversely dehiscent. Pollengrains globose or nearly so, spinulose, about 0.018 mm. in diameter. Pistil about half the length of the stamens, both curving upward

[2] Methods of obtaining Lemnaceae in pure culture have been described by Saeger (1930), Clark (1931), and Hopkins (1931).

from the edge of the leaf. Pistil flask-shaped, with funnel-shaped stigma. Seeds not observed. Upper epidermis with numerous stomata, lower epidermis and adjacent cells usually pigmented. Rhaphides and druses present in many cells throughout the plant.

No specialized resting or "winter" plants were observed sinking to the bottom of the substrate (as in *S.polyrrhiza*), but the plants became very small under poor growth conditions. This species is distinguished readily from *S. polyrrhiza* by its smaller size, fewer roots and veins, and more oblong leaf; and from *Lemna minor* (which it resembles in size) by the presence of more than one root per plant and by its more asymmetric shape. In pure culture, the flowers appeared after the exhaustion of certain nutrients in the water, but no fruit was developed. The vegetative growth of plants that are in bloom is retarded, and such plants are smaller (2.6 mm. ×1.4 mm.) than those actively growing.

Botany Department
University of Missouri

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Explanation of plate 13

Figs. 1–15. *Spirodela oligorrhiza.*

Figs. 1 & 2. Dorsal view of colonies showing venation, roots, and method of budding.

Fig. 3. Ventral view of plant in flower. *a* spathe. *b* basal stalk. *c* node. *d* daughter plant. *e* flap of bud pocket. *f* midvein. *g* root (severed). *h* bud pocket, flap of bud pocket removed.

Figs. 4 & 5. Young plant about 1 mm. long, dorsal view, showing part of basal bract. *a* point of attachment to parent plant. *d* dorsal portion of bract.

Figs. 6 & 7. Young plant about 1 mm. long, ventral view, showing part of basal bract, young roots, and buds. *a* point of attachment. *b* & *c* young buds developing into daughter plants. *e* young roots just before piercing the bract. *f* ventral portion of bract.

Fig. 8. Distal portion of root. *a* root cap.

Figs. 9, 11, 13 & 14. Floral parts emerging from edge of plant.

Fig. 10. Old, partially dried stamen.

Fig. 11. Young pistil appearing before stamens.

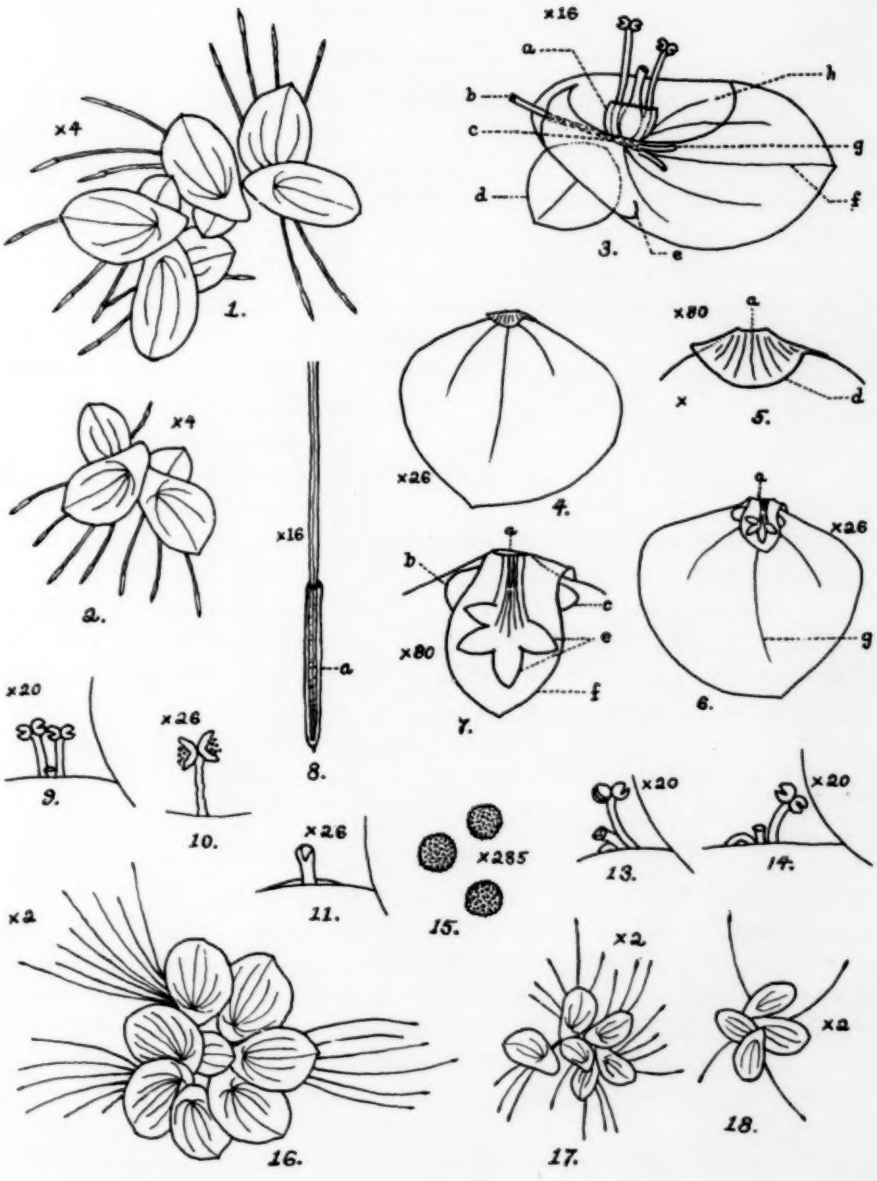
Fig. 15. Pollengrains.

Figs. 16–18. Comparison of three species of Lemnaceae.

Fig. 16. Colony of *Spirodela polyrrhiza*, roots shown on three of the plants.

Fig. 17. Colony of *S. oligorrhiza.*

Fig. 18. Colony of *Lemna minor.*



SAEGER: SPIRODELA OLIGORRHIZA

Pleistocene plants from Cuba

EDWARD W. BERRY

(WITH PLATE 14)

Included in the paleobotanical material from Cuba gotten together by the late Arthur Hollick and turned over to me by the New York Botanical Garden are two lots from the Pleistocene which are of especial interest.

The first of these was collected by Barnum Brown in 1911 and came from the celebrated hot spring of Chapapote at Baños de Ciego Montero in Santa Clara province and found in association with a Pleistocene mammal fauna.[1] The plants from this locality were subsequently identified by Percy Wilson of the N. Y. Botanical Garden and the woods by Prof. Saml. J. Record of the Yale School of Forestry. They comprise the following:

Pinus caribaea Morelet (3 cones)
Juniperus sp. (wood)
Mimusops emarginata (L.) Britton (fruit)
Conocarpus sp. (wood)

The second lot came from an asphalt pit 100 meters west of the Hamel well about 3 km. east of Sabanilla de las Palmas in Matanzas province and was collected early in 1933 by Doctors Dickerson, Bermudez and Richards of the Atlantic Refining Co. It comprises a number of pieces of asphalt-impregnated wood the identification of which has not been attempted, a considerable number of various sized fruits of *Spondias lutea* L. and a single fruit of *Chrysobalanus icaco* L.

Such of the foregoing as require comment will be taken up in the accepted systematic order.

PINUS CARIBAEA Morelet (figs. 14, 15)

There are three cones in the collection—a fairly complete unopened specimen, an opened specimen, and a third badly macerated specimen. The first two are figured. These were determined by Percy Wilson, and there can be no doubt regarding the identification. The species is supposed to occur near the coast of the United States from South Carolina to Louisiana, in the highlands of Central America and in the Bahamas, Cuba and the Isle of Pines, a geographical distribution, which if correct, is indicative of considerable antiquity for the species.

There is some confusion in the precise limits of the recent forms which have been referred to this species but this has no bearing on the present occurrence.

[1] Brown, Barnum. 1913. Some Cuban Fossils. Amer. Mus. Jour. 13: No. 5: 221–228.

The *Juniperus* wood from Chapapote spring presumably represents *Juniperus barbadensis* L., the common Bahaman and West Indian red cedar.

CHRYSOBALANUS ICACO Linné (fig. 11)

A single specimen of a drupe of this species is contained in the collection from the asphalt deposit. The modern species, which is widely distributed from southern Florida through the Antilles to northern South America, is essentially a coastal species. Leaves referred to the genus *Chrysobalanus* have been described at a number of geological horizons in various regions, but the only one of these that is absolutely beyond question is *Chrysobalanus eocenica* Berry[2] from the lower Eocene of southeastern North America, which is represented by both leaves and characteristic fruits.

SPONDIAS LUTEA Linné (figs. 1–10)

The most common fossils in the asphalt deposits are the fruits of this species. They are of all sizes and conditions of preservation due to the peculiar configuration of the stone of the drupe. This is irregularly ligneous, that is, its configuration is one of irregular conical elevations separated by rounded excavations. The stone is covered in life with a fibrosuberous filling, which may shrink on drying and fissure in a wholly irregular way, but which in the majority of cases shrinks transversely much more than longitudinally and splits into regular segments that give it the appearance of a tardily dehiscent capsular fruit. This condition is shown in figure 2 of a fossil fruit and in figure 8 of a recent fruit. With more or less maceration the outer coat becomes more or less eroded and this condition is shown in figure 1 of a fossil fruit and figure 7 of a recent fruit. Sections of fossil fruits showing two seed cavities are shown in figures 4–6 and similar sections of recent fruits are shown in figures 9 and 10. These sections also show more or less clearly the line of contact between the stone and the overlay. I cannot detect any differences in form or structure between the fossil and the recent fruits of *Spondias lutea* except that some of the fossils are more prolate, as in figure 4, than any recent fruits I have seen in a rather large series from different places.

The only other living species of *Spondias* in the Antillean region (*Spondias purpurea* L.) has fruits which average not more than two-thirds the diameter of those of *Spondias lutea* L. They are also much more prolate and almost twice as long as they are wide. The stone is less excavated. The flesh appears thinner and less suberous and dries to a wrinkled condition

[2] Berry, E. W. 1930. U. S. Geol. Survey Prof. Paper **156:** 73, *tf. 13, pl. 12, figs. 2–4.*

with no trace of the capsular-like shrinkage cracks which develop in *Spondias lutea*. It is true that I have seen only three specimens of the fruits of *Spondias purpurea*, and it may be that in a larger series all of the differential features enumerated above might not hold, but in any event the fossil fruits are very obviously different from those of this species.

The fruits of *Spondias lutea* are the most common objects in the beach drift throughout the Antilles and on both coasts of tropical America and the species also occurs in inland situations as well as in coastal situations. From the structure and occurrences as described above it follows that these fruits are very buoyant as Sloane pointed out in the late 17th century. It has not been found in the European drift although Guppy determined experimentally that it would float for at least 7 months. Viability is lost, however, after 2 or 3 months. Guppy seems to imply that the genus reached equatorial America from tropical West Africa but this does not seem to me to be the case.

The genus contains 6 or more existing tropical species all but one of which, *Spondias mangifera* Willdenow of the Indomalayan region, are represented in America and at least three of these are confined to America. Fossil species are rare. A leaf referred to this genus has been described from the Pliocene of eastern Brazil[3] and related fossil fruits have been described from the Old World Eocene[4] and Miocene[5] under the generic name *Spondiaecarpum*.

The occurrence of the fruits in the Pleistocene of Cuba sheds no certain light on whether the situation was coastal or inland, but the degree of erosion of some of the specimens and their association with *Chrysobalanus* rather favors a coastal interpretation.

Mimusops emarginata (Linné) Britton (fig. 13)

This species is represented by a transverse section of one end of the fruit with the features shown in figure 13. This came from the Chapapote spring, and I do not know how it happened to be cut or by whom, but it was presumably complete when collected. It shows several developed and traces of abortive seed cavities as well as the histology of the pulp. Undoubtedly the microscopic features could be made out if the fossil were sufficiently old or unique to repay the effort.

The recent form is a rather small tree found in dry situations and essentially a strand type. It ranges from southern Florida and the Bahamas

[3] Hollick and Berry. 1924. Johns Hopkins Univ. Studies in Geology, **5**: 74, *pl. 7, fig. 9*.

[4] Langeron, M. 1899. Soc. hist. nat. d'Autun, **12**: 453, *pl. 3, figs. 2, 4*.

[5] Menzel, P. 1913. Jahrb. k. preuss. geol. Landes. **34**: 6, *pl. 1, figs. 8–18*.

to Cuba and will doubtless be discovered eventually on other Antillean islands, since if the fossil is correctly determined it is a species of considerable antiquity. A rather similar species, *Mimusops sieberifolia* Berry,[6] occurs in southeastern North America as early as the lower Eocene.

SUMMARY

All of the described species, representing the families Pinaceae, Rosaceae, Anacardiaceae and Sapotaceae are still existing and common elements in the same region in which they occur fossil, so that they afford no evidence of changes in specific features or changes in geographic distribution which might indicate great antiquity. On the other hand the physical changes which took place in the Antillean region since late Tertiary times can hardly be regarded as sufficient to have brought about great changes in the flora; and these plants, like those I described some years ago from Trinidad,[7] could very well have existed in early Pleistocene times as well as at any subsequent time.

GEOLOGICAL DEPARTMENT
THE JOHNS HOPKINS UNIVERSITY
BALTIMORE, MD.

[6] Berry, E. W. 1916. U. S. Geol. Survey Prof. Paper 91: 339, *pl. 99, figs. 2; pl. 100, fig. 3.*

[7] Berry. E. W. 1925. U. S. Natl. Mus. Proc. 66: Art. 21.

Explanation of plate 14

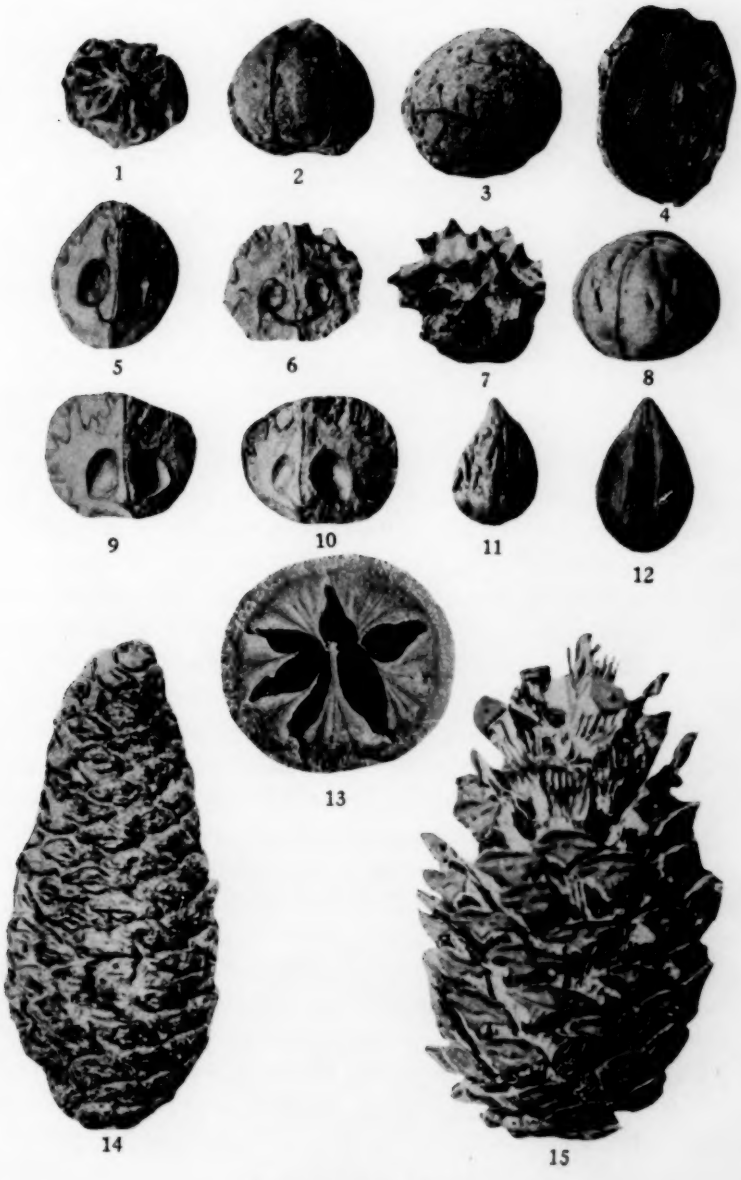
Figs. 1–10. *Spondias lutea* Linné. 1–6. Pleistocene. 7–10. Recent.

Figs. 11, 12. *Chrysobalanus icaco* Linné. 11. Pleistocene. 12. Recent.

Fig. 13. *Mimusops emarginata* (Linné) Britton. Transverse section of fruit.

Figs. 14, 15. *Pinus caribaea* Morelet.

All natural size.



BERRY: PLEISTOCENE PLANTS

The so-called "chemical stimulation" of Aspergillus niger by iron, zinc, and other heavy metal poisons

ROBERT A. STEINBERG

The rapid accumulation of papers dealing with the nutrition and stimulation[1] of *Aspergillus niger* had led to a condition, prior to the introduction of the method of nutrient purification, that made it almost impossible to decide upon the authenticity of much of the data and its interpretation. Since an increased interest is again being shown in this field and in similar studies with green plants, a few observations on recent developments might be of aid in helping to clarify the situation. A brief discussion of what is meant by stimulation with respect to chemical action is also included since so much confusion exists regarding its meaning that it has even been recommended by Kostytschew (1931. **2:** 327) that the term be no longer employed.

Limitations of space forbid discussion of the many papers in this field excepting to note that the majority of the earlier investigators adopted the view of Pfeffer that the effect of heavy metal salts on the fungus is due to partial poisoning or "chemical stimulation." In 1919, however, Steinberg succeeded, by means of a nutrient purification method which he developed, in obtaining such large increases in growth of *A. niger* with zinc and iron that the theory of "chemical stimulation" with respect to their action was no longer tenable. The data also, for the first time, gave really convincing evidence of the indispensable need of a fungus for zinc and for iron. Inhibition of spore formation could not, moreover, be attributed solely to zinc since it was shown that the increased acidity of the nutrient solution brought about by the fungus also participated. Also both growth and the effectiveness of zinc in aiding growth varied with the acidity. Tests with other "stimulants" gave negative results. The author, therefore, considered he had proved both iron and zinc indispensable for the fungus; and assumed the growth increases reported for other so-called "chemical stimulants" as also due to causes other than "chemical stimulation."

Beginning with 1927, Steinberg's data and technique, which had so far received but little attention, obtained ample confirmation through the work of Bortels, Roberg and Metz, whose data will be referred to subsequently. These investigators also came to the conclusion that iron and zinc are indispensable for the growth of *A. niger;* and that copper also seems necessary.

[1] "Stimulate" and its derivatives, when employed in this paper with reference to increase in vital activity by poisons, will be so indicated by quotation marks.

While "chemical stimulation" or "stimulation" has reference in this field specifically to increases in vital activity of an organism in the presence of sub-lethal doses of a poison, the same expressions are also used with other meanings. To stimulate means ordinarily, "To arouse to or to increase action in, by applying some form of stimulus"; without implication of inhibition or reference to nutrition. Many have used the term as synonymous with "increase."

The meaning assigned to these terms and their derivatives by Pfeffer (1893, p. 75) is as follows:—"Reizung liegt vor, wenn der von aussen oder von innen ausgehende Anstoss die Veranlassung gibt zu *irgendwelches* Aktionen, welche mit den im Organismus disponibeln oder erreichbaren Mitteln ausgeführt oder betrieben werden. Durch die Reizung können ebensowohl Tätigkeiten neuerweckt oder auch die schon vorhandenen Aktionen in neue Bahnen gelenkt werden." Stimulation, according to this concept, may be due to either internal or external stimuli and may manifest itself as either excitation or inhibition. The stimulant furnishing the stimulus does not supply any material or energy (i.e. act as a nutrient) in bringing about the response; although Pfeffer (1895) states elsewhere that nutrients may also furnish stimuli, as may a variation in concentration.[2] Stimulation may consist in arousing an activity anew or the original activity may be modified. The responses are usually but not necessarily such as are normally associated with the plant. While the stimulant furnishes no energy in bringing about stimulation, it must, evidently, require the expenditure of some energy, even if entirely disproportionate in magnitude to the response, to bring about the internal change or stimulus in the organism from which the response develops. A relation exists between degree of stimulus and magnitude of response.

"Chemical stimulation" refers specifically to those phenomena (Pfeffer 1895) in which, " . . . andere Thätigkeiten des Stoff- und Kraftwechsels werden offenbar durch kleinen Mengen . . . verschiedener, besonders auch giftiger . . . Körper *beschleunigt*. Theilweise dürfte sich um physiologische Gegenreactionen handeln . . . bei schädlichen und anderen Eingriffen hervorrüfen können"; catalysis, he states, might also play a part. Since Pfeffer (1897) also includes iron, it is evident that the "stimulant" may be either essential or non-essential. "Chemical stimulation," then, is any excitation in vital activity of an organism caused by toxicity. The increases are of presumably abnormal nature since due to abnormal condi-

[2] Increased growth through increased concentration, though ample material for the nutrition of the organism is already present, should be considered as a response to stimulation.

tions. The term does not include inhibition nor nutritive effects. The expression, toxicity, is generally used with reference to stimulative effects of inhibition.

The phenomena referred to usually as ion toxicity are seldom spoken of as "chemical stimulation" nor the compounds employed as "stimulants" or poisons. Nevertheless studies in this field do not have to do only with metabolism (unessential materials are also effective) but deal more especially with external chemical stimuli affecting the permeability and other regulatory mechanisms of the protoplast. Since the stimulus may be either excitation or inhibition; and since the stimulative effects of all substances and of concentration are included, "chemical stimulation," and chemical toxicity may be considered as limited phases of ion toxicity studies. It should be remembered however that in "chemical stimulation" it is assumed that the increased vital activity is caused by toxicity and is abnormal, whereas in ion toxicity it is assumed that increased vital activity is caused by elimination of toxicity and is normal.

The organism has been pictured as a system in unstable equilibrium, which, though it be in balance with its physical and chemical environment, is subject to internal stimuli, continually appearing in their normal sequence even in a constant environment, and to external stimuli; an extraordinarily complicated system of regulatory stimuli and metabolic responses. It might therefore prove advisable, in order to avoid confusion, to encourage the use of the terms, excitation and inhibition, with reference to stimulative or non-metabolic causes (Reize) only; just as the terms anabolism and catabolism, are used with reference to nutrition or metabolism (Stoff- und Kraftwechsel). It must be emphasized also that use of the term, stimulation, definitely implies a non-nutritive regulatory impulse that may result in normal as well as abnormal responses; whereas "chemical stimulation" refers to abnormal excitation only.

In the case of *A. niger* and zinc, which have served as the classic materials for the study of "chemical stimulation" for 63 years, the following reasons have been advanced for concluding that the increased growth is abnormal or "stimulative," instead of normal or nutritive. The fungus seems to make good growth and form spores in the absence of zinc. Many poisonous substances, cobalt, nickel, cadmium, iron, etc., have been reported to bring about similar growth increases. The growth increases found are relatively small—10 to 300 per cent. Spore formation is unfavorably affected. Lastly the cultures form "heavy, opaque and wrinkled" felts in the presence of zinc, whereas when zinc is omitted the felts are "translucent, slimy and smooth."

It is a mistake, to being with, to assume that "stimulants" *must* cause

inhibition of sporulation when they serve to aid growth. There are no specific data showing this to be a fact. Furthermore, there is much evidence showing that even with zinc there need be no inhibition of sporulation. Steinberg (1919) obtained results indicating that high concentration of magnesium sulphate (or traces of iron and copper which it might contain) and increased concentrations of iron phosphate counteract the harmful action of both zinc and high acidity upon sporulation. Also that ammonium hydroxide acts similarly, presumably by preventing an increase in acidity of the nutrient solution generally occurring in the presence of zinc. Results leading to the same conclusions have been reported by Bortels (1927), Roberg (1928, 1931) and Metz (1930). Roberg has done much to clear up this phase of zinc "stimulation" by recogniton of the elimination by iron of the harmful effect of both zinc and acidity upon sporulation.

The fact that only a moderate increase in growth took place when poisonous substances were added to the nutrient solution has also been accepted as proof that toxicity and not nutrition is the underlying cause of these phenomena. Data already in the literature will demonstrate however that this could only be true because of incomplete removal of heavy metals from the nutrient solution in the researches upon which this statement is based. Steinberg (1919, Exp't 36) found that in a complete nutrient solution containing zinc, the addition of iron may increase the growth of *A. niger* 4370 per cent. Similarly zinc when added to a complete nutrient solution containing iron may increase the growth of *A. niger* 230,900 per cent. Increases in dry-weight of these magnitudes can hardly be termed "stimulation."

Furthermore the objection to the nutritive interpretation, that good growth (about 300 mg. dry-weight) occurs in the absence of "stimulants" from the nutrient solution, can no longer be retained in the case of iron and zinc. The growth on an "iron-free" purified solution amounts, according to Steinberg (1919, 1920), to but 36.5–67.5 mg. dry-weight, that in a "zinc-free" purified solution to 0.5–12.5 mg. dry-weight. These figures refer to actual growth after deducting 3.5 mg. dry-weight of the inoculum. Comparing these figures with a maximum possible yield of about 1200 mg., it must be admitted that growth is almost entirely suppressed when iron or zinc is omitted.

Mention may be made at this point of the fact that in the presence of zinc the felts of *A. niger* become "opaque, heavy and wrinkled." These morphological changes have also been cited by many as evidence of abnormality and therefore "stimulation." It would seem sufficient to point out however that if zinc is essential for its growth, the felts of *A. niger* should become heavier when zinc is added, and probably more opaque

because of better nutrition. As the result of experience with this fungus, the inclination would be to associate the formation of "translucent and slimy" hyphae with lack of growth due to poor nutrition and to injury by chemicals. Similar hyphae, for example, are always found at the bottom of the culture flasks where oxygen is lacking. Often these conditions are associated with inability to form a felt upon the surface of the nutrient solution. The wrinkling of the felts is also probably due to improved nutrition.

Due to the many contradictory results obtained through the use of standard methods, only data obtained with a purified nutrient solution will be considered here in relation to the increase in growth or "stimulation" reported for many poisonous substances. In so doing one minimizes at least any likelihood of errors due to contamination of the solution, although of course increases due to other causes may still, if not carefully examined, be mistakenly held due to toxicity. Zinc is absent from the purified solution, moreover, to a degree never before attained. Nevertheless, under these conditions, which may result in an increased growth with zinc of about 230,000 per cent, not one of a total of eleven poisonous substances recently tested have been found capable of causing "stimulation." But one of the above substances, copper, has been found to increase growth appreciably and then only if zinc is also added. Copper, since it cannot be replaced by other elements and because it seems to be necessary for formation of black pigment in *A. niger* spores, is assumed to be essential. Poisons do not, it is evident, increase growth in the complete or almost complete absence of zinc nor, excepting copper, in the presence of an optimum concentration of zinc.

No increase in growth could be obtained by Steinberg (1919, 1920), using a purified nutrient solution, with sodium silicate, and salts of cobalt or uranium. Bortels (1927) could not, moreover, obtain "stimulation" of growth when using the method of nutrient solution purification with sodium silicate, arsenic, or salts of cobalt, manganese, aluminum and mercury either in the presence or absence of zinc nor Roberg (1928) with boron, iodine, arsenic or salts of uranium, manganese, and cadmium. Of the 14 poisonous substances listed as "stimulants" by Steinberg (1919), on the basis of data in the literature, it is to be noted that the most consistent and recent data indicate three (iron, zinc, copper) are essential, and seven (silicon, cobalt, uranium, manganese, cadmium, aluminum, mercury) are incapable of "stimulating" growth. Four (beryllium, nickel, lithium, fluorine) still remain to be tested by the method of nutrient purification.[3] Specificity such as exhibited by iron, zinc and copper is char-

[3] Since this paper was written the author has obtained experimental evidence demonstrating

acteristic of the biologically essential elements and seems to be dependent upon the limited range in properties of the elements that may successfully be used in the complicated system of reactions comprising the protoplasm.

In "chemical stimulation" it is assumed that with a progressive increase in the supply of a "stimulant," for example iron, growth is increased through nutrition until the optimum is reached. Above this point, however, is supposed to be another region of increasing growth due, not to nutrition, but to toxicity. Only above this second maximum does growth always show a decrease with further increase in iron. Growth in the nutritive range is considered normal, in the "stimulative" range morphologically abnormal. The ability of a "stimulant" to cause increased, if abnormal, growth in an optimum solution is definitely implied.

These growth increases have also been associated with *changes in balance of functions* whereby the direct inhibitory effect of toxicity on one function of the organism (sporulation) results in a secondary excitation of another (growth). Toxicity according to this view results in inhibition of reproduction, the materials conserved furnishing additional nutriment for an increase in mass. Excitation therefore need not enter at all into the increase in mass. This theory affords no explanation, however, as to the reason for non-utilization of much of the available nutriment in the so-called "normal" or "un-stimulated" culture, and its effective utilization in the "stimulated" culture.

Taking into consideration further the large number of possible "stimulants" and their wide differences in chemical constitution it does not seem plausible to postulate the existence of any growth mechanism sufficiently complex to be capable of bringing about the identical, or closely identical, responses known as "chemical stimulation" through individual reactions. The same growth mechanism must function in its orderly and normal processes with or without "stimulation." The probability is also that the presence of these heterogeneous materials within the cell could result in similar action only through destruction of normal cell constituents and their oxidation through normal respiratory processes. Since the increase in respiration by poisons has been reported to effect an increase in the economic coefficient with *A. niger*, thus conserving materials for growth in weight, a general destruction of cell materials need not, however, be considered. The data, moreover, discussed by Palladin (1923), indicating that for increased respiration through action of poisons, the cell must remain intact and that the enzymes concerned do not increase in effective-

the necessity of manganese, as well as of iron, zinc, and copper, for the nutrition of this fungus. None, however, of the other chemical elements just enumerated (including beryllium, nickel, lithium and fluorine) gave an increase in growth.

ness, would also tend to indicate that these phenomena are colloidal and take place at the boundary of the cell as in ion toxicity effects on permeability. Destruction, for example, of only a minute layer of the plasma membrane by "stimulants" so as to increase permeability to oxygen or carbon dioxide, or both, might lead to slight increases in growth through a more thorough decomposition of respiratory materials and conservation of a larger balance of plastic materials for growth in mass. The belief in similar increases in mass with toxicity is in the case of *A. niger* based on what now appears to be erroneous evidence. Increased acid production in the "stimulated" culture is also contrary to this hypothesis. There is no need, therefore, to assume the growth mechanism of the cell provides for stimulatory, catalytic, and other effects ("Gegenreactionen") matching in number the possibly innumerable and diversely constituted "chemical stimulants"; nor that conservation of material for growth in mass occurs.

A direct and positive test for "chemical stimulation" of growth is possible with an optimum nutrient solution for growth, since an increase in growth through any addition cannot under these conditions be ascribed to nutrition (essential substances or partial substitutions), or correction of ion toxicity of the solution. In the absence of positive evidence that the nutrient solution contains all essential compounds in optimum amount before addition of the "stimulant", it is necessary to demonstrate that the "stimulant" is free of elements essential for the organism or capable of substitution for an essential element present in suboptimal amount, and that ion toxicity has not been corrected through addition of the poison.

The method of nutrient solution purification from heavy metals has proved the best means of obtaining accurate data in this field. The difficulty in obtaining compounds of sufficient and constant purity solely by means of recrystallization, or in different lots of commercially prepared chemicals, is well known and amply illustrated in the literature of this field. Data by Roberg (1928) affording a comparison between his own and others' results with the purification method show, however, exceptionally good agreement for physiological work of this character when it is taken into consideration that chemicals, glassware, etc. of entirely different origin were utilized.

DEPARTMENT OF AGRICULTURE
BUREAU OF PLANT INDUSTRY
WASHINGTON, D. C.

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Some physiological effects of girdling northern hardwoods[1]

HENRY I. BALDWIN

INTRODUCTION

In connection with a project for studying the effects of the release of the conifer understory by girdling the overtopping hardwoods, observations were made on the behavior of the hardwoods following girdling. The purpose of these observations was to determine the effectiveness of girdling in killing the decadent hardwoods, and how soon they would die and be removed from competition with the conifers.

A thorough review of the extensive literature on girdling will not be attempted here. T. Hartig (1858) was one of the first to observe the excess of food reserves above the ring over that below. He girdled young oaks in summer and on testing the wood for starch the following spring, found it had disappeared below the ring. Du Sablon (1905) showed that the bark must have some important function in food conduction. A large number of ringing experiments have been made, especially in horticulture; many give conflicting data on the effect of ringing in interrupting the translocation of foods. The later work of Curtis (1929) points to both upward and downward movement of carbohydrates, and to some extent inorganic nutrients in the phloem. Mason and Maskell (1928) in an exceptionally thorough investigation of translocation in the cotton plant found that ringing caused a blocking of downward transport and an accumulation of carbohydrates in the wood above the ring. The bulk of the present evidence indicates that the greater part of elaborated food material moves downward through the phloem. Many of the results of girdling experiments have been contradictory, however, and therefore the present data on the relative amounts of food reserves in girdled trees may be of interest. Furthermore, comparatively few observations have been made on the northern hardwoods, yellow birch (*Betula lutea* Michx.), beech (*Fagus grandifolia* Ehr.) and sugar maple (*Acer saccharum* Marsh.) and accompanying species. The work was carried on near Cupsuptic Lake in northwestern Maine, and in northern New Hampshire in 1925 and 1926. It should be borne in mind that these observations were incidental to the main project, and hence are very fragmentary.

[1] The results presented here are taken from reports of experiments on girdling hardwoods carried on from 1924–1932 for the Brown Company, Berlin, N. H., through whose courtesy the data is made public.

METHODS

1. *Girdling.* Trees were girdled by chopping rings around the bole at waist height. Three methods were used: (a) Notching, or chopping out a clean notch one to two inches into the sapwood, similar to the cut made when felling a tree. The notch was made completely around the tree. This method, while most certain of severing all phloem strands, and in addition, cutting into the xylem, demanded more skill, and was generally more expensive than others. (b) Peeling, or stripping the bark on a belt six inches to one foot wide around the tree. This was easiest to accomplish, and most certain of results when done in spring. (c) Hacking, or frilling the bark by downward cuts of the axe. This was cheapest, but found to be unreliable, since phloem strands would occasionally be left intact if the chops were not completely overlapping. Therefore it was soon superseded by double hacking, which has given the best satisfaction from all points of view. While trees were girdled at all seasons of the year for experimental purposes, the superiority of late winter from the standpoint of cheapness and organization of the work made other seasons out of the question. All observations here reported refer to trees girdled in February and March.

2. *Observations.* General notes were made of the condition of the trees whenever they could be visited. These were correlated with the data on the practical aspects of girdling, such as what species and sizes were most difficult to girdle. On sixteen one-acre permanent plots all trees were numbered, mapped and crown projections plotted. All trees were classified as to vigor and condition before girdling, and these observations compared with those made at intervals after girdling. General observations were also made on the larger areas of commercial girdling.

3. *Sampling.* One and two years after girdling blocks four inches high were sawed out of girdled and control trees one foot above the girdle and one foot below the girdle. These samples were taken during freezing weather, and placed in large mason jars for transport to the laboratory. There they were chipped, moisture content determined, and dextrose and total sugar content determinations made for each sample, using procedure recommended by the Association of Agricultural Chemists Methods of Analysis, 1925 (page 190).

RESULTS

The first growing season. The first observation was the drying of exposed sapwood, followed by the bleeding of sap from the cut trees with the advent of the maple sugar season. When the snow disappeared in May and warmer weather arrived fungous growths appeared on the sap. Birch trees were especially conspicuous because of a brilliant pink fungus. The

fungi consisted of a group of moulds, yeasts and bacteria, commonly known as slime flux. Toward June all bleeding and growth of fungi ceased, and the exposed sapwood felt dry to the touch.

Opening of the leaves and blossoming took place without any noticeable difference from control trees.

Autumnal coloration in girdled trees occurred from two to four weeks in advance of control areas. This was especially striking, the red and yellow

TABLE 1

Moisture content of girdled trees in per cent (based on oven-dry weight)

LOCATION OF SAMPLE	YELLOW BIRCH		SUGAR MAPLE		BEECH		AVERAGE OF ALL SPECIES			AVERAGE OF ALL METHODS AND LOCATION OF SAMPLE		
	NOTCHED	PEELED	NOTCHED	PEELED	NOTCHED	PEELED	NOTCHED	PEELED	AVERAGE OF BOTH METHODS	YELLOW BIRCH	SUGAR MAPLE	BEECH
ONE YEAR AFTER GIRDLING												
Above cut	14.0	20.2	9.1	15.4	13.9	16.5	12.3	17.3	14.8	17.1	12.2	15.2
Below cut	20.1	16.7	13.9	15.4	8.9	10.8	14.3	14.3	15.3	18.4	14.6	9.8
Controls[a]	16.8	16.8	17.6	17.6	13.6	13.6	16.0	16.0	16.0	16.8	17.6	13.6
										17.5	13.4	12.5
TWO YEARS AFTER GIRDLING												
Above cut	18.3	14.5	8.4	12.8	17.8	14.7	14.8	14.0	14.4	16.4	10.6	16.2
Below cut	17.6	13.8	11.4	17.8	20.1	20.0	16.3	17.2	16.7	15.7	14.6	20.0
Controls[a]	19.1	19.1	12.7	12.7	19.6	19.6	17.1	17.1	17.1	19.1	12.7	19.6
										16.0	12.6	18.1

[a] But one control sample was taken for each species.

foliage standing out conspicuously against the deep green of the forest outside the plots. By September some few trees had died, but most trees showed little effect of the girdling except premature coloration of the leaves. On analysis, it was found that about one-third of the trees denoted as "poor" in vigor before girdling had actually improved and been given a higher rating. Girdling may have so trapped reserve foods in the bole as to nourish dying branches better than before. Such effects must, of course, be temporary. Similar conditions have been observed after spring forest fires which girdled, but did not kill the trees outright.

Sprouting from the edge of the ring occurred in a few trees, chiefly beech.

No difference in the seed production could be ascertained, but no detailed measurements were made. All trees, whether girdled or not, bore profuse crops of seed.

The second growing season. Many trees showed marked weakening in vigor the second season. Leaf development was poorer; both the average leaf size was smaller, and many leaves withered and dropped soon after opening. Autumnal coloration again was premature. In some cases seeding was abundant. The more sensitive species such as black ash, black cherry, beech and paper birch were nearly all dead by the second season.

Relative sensitivity to girdling in relation to physical difficulty of girdling

operation. A relation was noted between the physical ease or difficulty of cutting into the tree and the promptness with which the trees died. This conclusion was based on a tally of trees on sample plots in September, 1925, one growing season after girdling, and on studies of the time re-

TABLE 2

Moisture content of girdled trees in per cent of control trees

LOCATION OF SAMPLE	YELLOW BIRCH		SUGAR MAPLE		BEECH		AVERAGE OF ALL SPECIES			AVERAGE OF BOTH METHODS		
	NOTCHED	PEELED	NOTCHED	PEELED	NOTCHED	PEELED	NOTCHED	PEELED	BOTH	YELLOW BIRCH	SUGAR MAPLE	BEECH
ONE YEAR AFTER GIRDLING												
Above cut	83.3	120.5	51.5	87.5	101.0	120.5	78.6	109.5	96.0	101.9	69.5	110.2
Below cut	119.0	99.1	79.0	87.5	65.3	79.1	87.7	88.5	88.1	109.0	83.2	72.2
										105.4[a]	76.4[a]	91.4[a]
TWO YEARS AFTER GIRDLING												
Above cut	96.0	75.5	66.1	100.2	91.0	75.0	84.3	83.5	83.9	85.7	83.1	83.0
Below cut	92.5	72.1	89.7	140.0	102.5	102.1	94.9	104.7	99.8	82.3	114.8	102.3
										84.0[a]	99.0[a]	92.6[a]

[a] Average of above and below cut.

quired to girdle each tree. The softer woods, comprising the species more intolerant of shade succumbed first. These were the species which furnished the easiest chopping. Many of these species are relatively short-lived, and

TABLE 3

Moisture content of girdled trees above the ring in per cent of content below the ring

	YELLOW BIRCH		SUGAR MAPLE		BEECH		AVERAGE OF ALL SPECIES			AVERAGE OF BOTH METHODS		
	NOTCHED	PEELED	NOTCHED	PEELED	NOTCHED	PEELED	NOTCHED	PEELED	BOTH	YELLOW BIRCH	SUGAR MAPLE	BEECH
One year after girdling	69.5	121.0	65.2	100.0	156.1	152.5	96.9	124.5	110.7	95.2	82.6	154.3
Two years after girdling	104.0	105.0	73.8	72.0	88.4	73.5	88.7	83.5	86.1	104.5	72.9	80.9

are not as severe competitors of the desirable conifers as the more tolerant hardwoods.

Moisture content of girdled trees. The results of analyses of samples taken from random trees one and two years after girdling are given in Tables I–III. Girdled trees did not differ markedly from control trees in moisture content during the first two winters following girdling. In fact there was generally greater range between different control trees different years than between controls and girdled trees (Table I). Obviously many more trees would have to be sampled to obtain conclusive data. The present material suggests a lower water content on the average for girdled trees. During the first year there was usually higher water content above

the ring than below, while the second year this condition was reversed. Peeled trees averaged a higher water content than notched trees, reflecting the greater interruption of xylem in notched trees.

Sugar content. In Table IV are given sugar contents in both invert

TABLE 4

Analyses of girdled trees

LOCATION OF SAMPLE	WATER CONTENT PER CENT		WEIGHT OF SOLUBLE CARBOHYDRATES IN MG. PER 20 GM. DRY WOOD INVERT SUGAR AND SUCROSE[a]		DEXTROSE[a]	
	1-yr.	2-yrs.	1-yr.	2-yrs.	1-yr.	2-yrs.
			YELLOW BIRCH NOTCHED			
Above ring	14.0	18.3	230.4	22.1	230.0	23.6
Below ring	20.1	17.6	0.3	2.3	0.3	4.7
			YELLOW BIRCH PEELED			
Above ring	20.2	14.5	184.8	1.1	196.0	3.0
Below ring	16.7	13.8	26.8	7.0	35.6	9.2
			YELLOW BIRCH CONTROL			
	16.8	19.1	61.6	48.2	78.4	48.3
			SUGAR MAPLE NOTCHED			
Above ring	9.1	8.4	216.8	8.1	227.2	10.4
Below ring	13.9	11.4	6.8	0.8	16.4	2.0
			SUGAR MAPLE PEELED			
Above ring	15.4	12.8	231.2	76.9	240.0	76.0
Below ring	15.4	17.8	6.4	27.3	16.0	28.5
			SUGAR MAPLE CONTROL			
	17.6	12.7	104.8	86.6	120.0	85.3
			BEECH NOTCHED			
Above ring	13.9	17.8	0.0	192.3	0.0	187.8
Below ring	8.9	20.1	4.3	10.7	6.6	12.6
			BEECH PEELED			
Above ring	16.5	14.7	20.0	131.2	29.0	128.3
Below ring	10.8	20.0	54.8	5.7	62.0	7.9
			BEECH CONTROL			
	13.6	19.6	58.0	43.9	65.2	44.4

[a] Computed from Munson and Walker's Tables.

sugar and dextrose, as computed from Munson and Walker's tables. It will be observed that the contents in each class of sugars follow one another very closely, and any conclusions for one group apply equally well for the other. Accordingly figures for dextrose only were used in computing Table V which shows more clearly the comparison between girdled trees and normal trees.

DISCUSSION

The water content of girdled trees was less, but showed little difference from ungirdled trees, and the difference was less the second year than the first. The fact that water contents showed as much difference as they did suggests that the girdling even by peeling, with drying out of the surface of the sapwood caused an interruption of the sap stream, either by clogging with air, or actually killing part of the water conductive tissue. The part played by this influence on water conduction may be of great importance in causing the death of the tree than would be at first supposed.

TABLE 5

Dextrose content of girdled trees in per cent of control trees

LOCATION OF SAMPLE	YELLOW BIRCH		SUGAR MAPLE		BEECH	
	NOTCHED	PEELED	NOTCHED	PEELED	NOTCHED	PEELED
	ONE YEAR AFTER GIRDLING (1926)					
Above cut	293.2	250.0	189.3	200.0	0.0	44.4
Below cut	0.4	45.4	13.6	13.3	10.1	95.0
Controls	100.0	100.0	100.0	100.0	100.0	100.0
	TWO YEARS AFTER GIRDLING (1927)					
Above cut	48.8	6.2	12.2	89.1	423.0	288.9
Below cut	9.8	19.0	2.3	33.3	28.4	17.8
Controls	100.0	100.0	100.0	100.0	100.0	100.0

Experiments in dyeing living trees showed that in virgin forest hardwoods a very narrow shell of sapwood was used in sap conduction.

In both seasons water contents were generally highest where there was least sugar, and where evidences of decay were most prominent. From the tables it will be noted that a conspicuously high water content above the cut occurred in beech one year after girdling, when a very low sugar content was also observed. Therefore decay is indicated as the cause of high water content. The higher water content above the ring than below is at variance with the reputed effect of girdling on crypress and teak, as well as other tropical trees, and suggests that girdling would be of no use in increasing the buoyancy of hardwood for river-driving. This agrees with the findings of Curtis.

Beech was an exception and apparently behaves differently than yellow birch and maple both when notched and peeled. The sugar contents were almost the exact opposite of the other species, low the first year and extremely high the second; higher below the cut the first year, and above the cut the second. These first year's results strongly suggest the activity of root suckers in keeping the old trunk supplied with carbohydrates. Presence of decay in the samples may have had some influence on the sugar

analyses. Differences in the root system, and silvical characteristics are probably also responsible.

The water content of beech compared to the other species may be due to the restriction of actively conducting xylem in beech to a narrower zone near the bark, than is the case with yellow birch and sugar maple. This is not fully proven, but experiments in injecting dyes into living trees at Dummer, New Hampshire in 1925 point to this as a possible explanation. This might also explain the retention of a large amount of water the first year after girdling, had transpiration been cut off; but it was observed that all beeches from which samples were sawed were in full leaf during the first growing season. Beech leaves are, however, heavily cutinized, and yet were observed to be partly wilted in late summer, which would have tended to close the stomata and reduce transpiration. It is possible that beech was so severely affected by girdling that forces tending to cause sap rise were impaired. In other species transpiration may have tended to pump dry the outer layers of the sapwood.

Sugar contents follow opposite trends from water contents. Yellow birch and sugar maple showed huge accumulations of sugar above the cut as compared to parts of the same tree below the ring, or to control trees. There was usually 20 to nearly 300 times as much above the cut as below and 2 to 3 times as much above the cut as in control trees of the same species. This agrees well with what other investigators have found, and confirms the usually accepted theory that the bulk of the carbohydrates move down in the phloem. The excess of sugars above the cut was quickly discovered by porcupines, who gnawed the bark of large numbers of trees, above the cut exclusively. Beech again showed quite contrary results from the other trees tested. In the case of notched beech, no sugar whatever was found above the ring the first year. Possibly the sugar above the ring was withdrawn to a large extent for starting growth; when the leaves opened and shortly thereafter, water conduction may have been so restricted that stomata were kept partially closed, and little carbon was assimilated. Stored food was depleted, and little or none laid up for the next season. The second season most of the beeches sent up small sprouts from the bottom of the cut. This, however, does not explain the higher sugar content above the ring observed in the second winter.

The results do not show conclusively whether notching or peeling is more effective in killing the tree, but there is little doubt that notching causes the more severe injury. It is curious to note that in sugar maple the sugar contents below the girdle the first year should have been almost identical for both methods, while in other cases notching was more effective in reducing the content below the ring as compared to peeling. The

second year this is shown also in sugar maple. This comparison between peeling and notching suggests that some carbohydrates may possibly be carried down in the outer layers of xylem.

The sugar contents reflect the ability of the trees to remain alive after girdling, and agree with the observed relative vitality of different species. Beech was thus rated considerably lower than the other two species in resistance to girdling. Trees with least sugar are apparently most sensitive to girdling. This is not in complete agreement with the accepted grouping of trees by their reserve foods; beech and maple are considered predominantly starch trees while birch is predominantly a fat-reserve tree. The indications were the first year that beech would succumb promptly, but the presence of root suckers may account in part for observed exceptions.

The premature coloration of the leaves might possibly have had some connection with a damming up of sugar in the upper part of the bole, which would have led to excess development of anthocyanin pigments, and coupled with reduced sap flow, caused premature development of the abscission layer.

SUMMARY

Observations are reported on the condition of girdled hardwoods during the first two years after girdling. Girdling was done in winter. These were supplemented by analyses of samples cut from trees one and two years following girdling.

1. Three to four years were required for girdled hardwoods to die completely. Some species died the first year. About a third of the trees which seemed low in vigor before girdling seemed to have been temporarily benefited the first summer.

2. Short-lived, intolerant and soft-textured species succumbed more rapidly than long-lived, tolerant, and dense-wooded species.

3. The most noticeable change in the trees the first season was premature autumnal coloration.

4. Girdled trees had about the same moisture contents as normal trees, usually slightly less.

5. Moisture content above the ring was about 10 per cent higher the first year, and 10 per cent lower the second year after girdling, as compared to the content below the ring.

6. A relatively high moisture content was found where the sugar content was low, and vice versa.

7. Invert sugars and sucrose showed the same general distribution as dextrose.

8. The first season after girdling abnormally large per cents of sugar

were trapped above the girdle. There was 20 to 300 times as much sugar above the cut as below, and 2 to 3 times as much as in normal trees.

9. Notching was more effective than peeling in causing carbohydrates to be concentrated above the cut. Interruption of the sap stream from carrying reserves up from the roots may also account for low sugar content below the cut.

10. Two years after girdling, sugar reserves were much depleted and were less even above the cut than in normal trees.

11. Beech differed from yellow birch and sugar maple in the relative distribution of sugar and water, and the results were generally erratic for this species.

12. The amount and distribution of carbohydrate reserves seems to be correlated with the resistance of the various species to injury by girdling. Trees which showed visible injury in foliage, etc., most promptly, also showed depletion of food reserves, and abnormality of water content.

Department of Forestry
Pennsylvania State College

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Field and herbarium studies. II.

LOUIS WILLIAMS

This paper is the second in a series based upon studies made at the Rocky Mountain Herbarium. The new names in *Lepidium* are proposed as a result of studies made in revising the genus for a new Flora now in preparation.

Lepidium Nelsonii sp. nov. Bienne aut perenne caducum; caulibus compluribus ex corona, 2–4 dm. altis, ramosissimis ex medio sursum, denso pubescentibus crinibus erectis; foliis oblongis vel linearibus, serratis, lacinatis aut pinnatifidis, utrinque pubescentibus; inflorescentia densa, in fructu multo elongata; petalis nullis aut perparvis; sepalis perparvis, albis; staminibus 2; stigmate sessili; silicula pubescente, circa 3 mm. longa; embryone notorrhizo.

Ascending biennial or short-lived perennial. Stems several from the crown, 2–4 dm. high, much branched from the middle upward, densely pubescent with erect hairs; leaves oblong to linear, serrate, laciniate or pinnately parted, moderately harsh pubescent on both surfaces, the cauline sessile; inflorescence dense, much elongated in fruit; petals absent or every minute; sepals minute, about 0.5 mm. long, white; stamens 2; stigma sessile in the notch of the silique; pubescent, orbicular, about 3 mm. long and a little less wide; pedicels divaricate, about 3 mm. long, cylindric; cotyledons incumbent.

Type, *Aven Nelson 11,417*, collected May 25, 1931, in low hills around Frijoles, New Mexico. *L. Nelsonii* is the most pubescent of the known southwestern species, from *L. hirsutum* Rydb. it can be easily separated by the pubescent siliques, from the forms of *L. virginicum* L. by the cotyledons.

Lepidium tenellum sp. nov. Perenne adscendens; caule 2–4 dm. longo, gracili, puberulo aut infra glabro; foliis basalibus oblongis, 1–3 cm. longis, incisis, petiolo gracili; foliis caulinis superioribus oblanceolatis, integris, inferioribus saepe incisis; inflorescentia ante anthesin densa, in fructu valde elongata, 4–7 cm. longa; pedicello reflexo, 5–6 mm. longo; calyce pubescente, ovato, albo aut saepe ad marginem purpureo, 1 mm. longo; corolla alba, orbiculari, 2 mm. longa; staminibus 6; silicula glabra, 3 mm. longa, 2.5 mm. lata, suborbiculari, margine alata; incisura fere obsoleta; stylo circa 1 mm. longo, valde exserto; stigmate subcapitato.

Ascending from large perennial clumps. The stems 2–4 dm. long, minutely puberulent or the lower part glabrous, very slender; basal leaves oblong, deeply incised, about 3 cm. long, the petiole slender, longer than the blade; upper cauline leaves oblanceolate, entire, almost sessile, the lower cauline leaves often incised or entire, 1–3 cm. long, petiolate, the petiole almost as long as the blade, often winged; inflorescence crowded before anthesis, much elongated in fruit; raceme lax, 4–7 cm. long; pedicels reflexed, spreading, 5–6

mm. long; sepals sparingly pubescent, ovate, white or often purple margined, 1 mm. long; petals white, orbicular, 2 mm. long, clawed, the claw exceeding the calyx; stamens 6; silique 3 mm. long, 2.5 mm. wide, glabrous, suborbicular, wing-margined; the notch almost obsolete; style about 1 mm. long, much exserted; stigma subcapitate.

Type, *Edwin B. Payson 1033*, July 8, 1917, in "Large perennial clumps in rock crevices near the R.R., Black Canyon of Gunnison, Colorado." Easily distinguished from the other Rocky Mountain Lepidiums by the very slender ascending stems and the lax, few fruited racemes. Distributed as *L. scopulorum?* Jones.

Lepidium tortum sp. nov. Perenne ex rhizomate magno; caulibus adscendentibus aut rectis, 20–40 ex corona, 1–3 dm. altis, puberulis, in aetate glabrescentibus, ramosissimis, ad nodos angulosis; foliis caulinis linearibus, integris, breviter acuminatis, 2–6 cm. longis; inflorescentia densa, in fructu usque ad 8 cm. longa elongata; sepalis albis, oblongis, 2 mm. longis; pedicellis 5–7 mm. longis, cylindratis, pubescentibus, divaricatis; silicula glabra, ovata, circa 3 mm. longa, 2 mm. lata; incisura evidente; stylo longo exserto, 1 mm. longo; stigmate globoso; seminibus 1.5 mm. longis; embryone notorrhizo.

Perennial from a large root-stock. Stems ascending or erect, 20–40 from the crown, 1–3 dm. tall, puberulent, becoming glabrous in age, much branched the whole length, angled at the nodes; cauline leaves linear, entire, short-acuminate, 2–6 cm. long; basal leaves not seen; inflorescence dense, racemes elongated in fruit, up to 8 cm. long; pedicels 5–7 mm. long, cylindric, pubescent or in age glabrous, divaricate; sepals white, oblong, 2 mm. long; petals white, ovate, 3 mm. long, claw 2 mm. long; silique glabrous, about 3 mm. long, 2 mm. wide, ovate, notch apparent; style long exserted, 1 mm. long; stigma globose; seed 1.5 mm. long, ovate, hyaline winged only near point of attachment, developing a gelatinous sheath when boiled; cotyledons incumbent.

Type, *L. N. Goodding 2281*, May 4, 1905, on ridges and slopes near Las Vegas, Nevada. Other collections are: *A. O. Garrett 5976*, July 23, 1931, west of Hawksville, Wayne C., Utah and *5980*, Wayne Co., Utah, *5930* Emery Co., Utah. Related to *L. alyssoides* Gray, it may be readily separated from that species by the long exserted style and the much angled stems, giving a ragged appearance to the plant.

Horkelia sabulosa (M. E. Jones) comb. nov.
Potentilla sabulosa M. E. Jones. Proc. Calif. Acad. II. **5**: 680. 1895.
Ivesia sabulosa M. E. Jones. l.c. As a synonym.
Comarella sabulosa Rybd. Mem. Dep. Columbia Univ. **2**: 157. 1898.

Potentilla albiflora sp. nov. Perennis humilis, 10–15 cm. alta; radice magna radiculis multis fibrosis; corona foliosa, ramis compluribus ex quaque corona; foliis trilaminatis, 5–15 mm. longis, 4–10 mm. latis, supra medium

crenatis breviter piloso-pubescentibus; foliis caulinis variis; petiolis foliorum in basalium gracilibus, 6–12 cm. longis, breviter piloso-pubescentibus; inflorescentia cymosa pauciflora; lobis calycis acutis, 3 mm. longis; corolla alba, lateobovata, 3 mm. longa; bracteis lanceolatis, 2 mm. longis, glanduloso-pubescentibus; acheniis circa 20 in quoque capite conico, glabratis.

A low alpine (?) perennial, 10–15 cm. tall. Roots large, bearing many small fibrous roots; crown leafy, leaves reaching almost to the inflorescence by a slender petiole, several flowering branches from each crown; leaves trifoliate, the middle leaflet 10–20 mm. long, 6–14 mm. wide, the lateral leaflets smaller, sessile or very short petiolulate, crenate above the middle by ovate lobes about 1 mm. long, short pilose-pubescent on both sides, that of the upper surface thicker and somewhat appressed; stem leaves various, some small and entire, 3–6 mm. long, 1 mm. wide, sessile, some short petiolate, trifoliate, the leaflets oblong and entire or tridentate at the apex, 8–12 mm. long, 4–6 mm. wide; petioles of the basal leaves slender, striate, 6–12 cm. long, moderately short pilose pubescent; inflorescence a few-flowered cyme; calyx lobes acute, gradually widening to the base, pilose-pubescent, 3 mm. long; petals white, broadly obovate, 3 mm. long, barely equaling the calyx; bracts lanceolate, 2 mm. long, pubescent and often ciliate with short glandular hairs; achenes about 20 in each cone-shaped head, about 1 mm. long, glabrate.

Type, *L. N. Goodding 1045*, near Fort Grant, Arizona on rocky, alpine slopes, June 15, 1912. Not closely related to any species known to the writer; in aspect resembling *P. maculata* Pourret, from which it differs in having only 3 leaflets which are not so deeply toothed and a white corolla, as well as a different geographical distribution.

Potentilla rubida sp. nov. Perennis erecta, gracilis, pauciflora, 5–8 dm. alta, ex rhizomate crasso, glanduloso—pubescens; foliis basalibus 5–6 digitatis; petiolis 1–3 dm. longis; foliolis sessilibus, oblongis aut oblongo-oblanceo latis, 2–7 cm. longis, serratis praeter mediam partem; stipulis magnis, 2–4 cm. longis, 5 mm. latis; foliis caulinis similibus sed minoribus; calyce 7 mm. longo, lanceolato-acuminato, pubescente et glanduloso aut glabro; corolla rubida, petalis obcordatis, 7–10 mm. longis, 5–8 mm. latis; staminibus circa 20; pistillis numerosis.

Erect, slender, few-flowered perennial 5–8 dm. tall, from a thick rootstock. Usually only one stem from each root, glandular-pubescent, more so above than below, scattering hairs near the base; basal leaves 5–6 digitate; petioles 1–3 dm. long, slender, glandular-pubescent; leaflets sessile, oblong to oblong-oblanceolate, 2–7 cm. long, sharply serrate for half or three-fourths of their length, minutely glandular on both surfaces, the veins on the lower surface prominent, pubescent with long hairs; stipules large, 2–4 cm. long, 5 mm. wide, sheathing, adnate to the petiole, having a linear-acuminate lobe on each side 6–15 mm. long, pilose; stem leaves similar but smaller, the petioles

short or the upper almost sessile, the stipules broad and often with one or more acute lobes; calyx lobes lanceolate-acuminate, about 7 mm. long, softly pubescent and minutely glandular or almost glabrous; bracts equaling the calyx, linear-acuminate; corolla dark purple, the petals obcordate, 7–10 mm. long, 5–8 mm. wide, the petals in the bud pustulate, the pustules containing a dark red liquid; stamens about 20, inserted on the reddish disk; pistils numerous.

Type, *C. H. T. Townsend* and *C. M. Barber 49*, in part, July 4, 1899, collected near Colonia Garcia, Chihuahua, Mexico. Distributed as *P. Thurberi* Gray, to which it is most nearly related; it may be distinguished by the oblong stipules which are not toothed but have two linear, lateral lobes, the leaflets are oblong to oblong-spatulate not obovate, the sepals are lanceolate-acuminate not triangular-acute.

Parosela Paysoniae sp. nov. Perennis humilis lignea, 2–3 dm. alta; caulibus multis ex radice, ramosis, denso sericeis ex medio sursum, glandulis nigris aut flavis punctatis; foliis 1–3 cm. longis, imparipinnatis 3–6-jugis; foliolis 5–8 mm. longis, 2–3 mm. latis, glanduloso-punctatis, dense sericeis; inflorescentia conferta, oblonga, 2–3 cm. longa, 1 cm. lata; staminibus 10, filamentis monadelphis; calyce circa 5 mm. longo, sericeo, nonglanduloso; corolla purpurea, circa 6 mm. longa; legumine sericeo, punctato-glanduloso; semine uno; stylo 6–7 mm. longo, ad basin pubescente, sursum glabro.

Low woody perennial, 2–3 dm. tall. Many stems from the base, branching almost their entire length, glabrous and roughened near the base, becoming densely sericeous from the middle upward, dotted with black or yellow glands the full length; leaves 1–3 cm. long, odd pinnate with 3–6 pairs of leaflets; leaflets oblong-oblanceolate, densely glandular-punctate, sericeous on both surfaces, 5–8 mm. long, 2–3 mm. wide; inflorescence crowded, oblong, 2–3 cm. long, 1 cm. wide; stamens 10, monadelphous; filaments united two-thirds their length; calyx sericeous, about 5 mm. long, the subulate teeth 2 mm. of this, not glandular, sessile on the rachis; corolla purple, the keel united half its length, saccate, long clawed; wings and banner not seen; pods sericeous, at least when immature, glandular-punctate, one seeded; style 6–7 mm. long, pubescent at the base, glabrous upward.

Lois B. Payson 37, September 27, 1931, rocky slopes near Carlsbad Caverns, New Mexico. Related to *P. lanata* (Spreng.) Britt., from which it differs in having a more dense and broader inflorescence, woody stems and the absence of glands on the calyx.

ROCKY MOUNTAIN HERBARIUM
UNIVERSITY OF WYOMING
LARAMIE, WYOMING

Inheritance of cotyledonary characters in Cucurbita Pepo

GARDIS B. THAYER

(WITH TEXT-FIGURE)

Comparatively little work has been done on the inheritance of cotyledonary characters. Mendel (1865) found that the yellow color of the cotyledon in peas was dominant over green and that there was a difference of a single factor between these traits. Hill (1925) reported that in *Digitalis* "the F_1 hybrids between species with differing types of cotyledons show strong matroclinous tendencies," but that "matrocliny is not complete, since the influence of the pollen parent is seen in the ratio of the width to the length of cotyledons." He explained this matrocliny as due to the relation between the maternal seed coats and the developing embryo. Michaelis (1931) confirmed Hill's results. Focke (1881) observed that in *Nymphaea* species hybrids the cotyledons resemble those of the female parent. The inheritance of cotyledonary size is complicated somewhat by heterosis. Thus Wingard (1927) found that bean seeds which arose through cross pollination were larger and had larger cotyledons than those which arose by self pollination. The results of Rosa (1926), however, indicate that in melons there is no significant difference in size between seeds arising from the two types of pollination. It is reasonable to expect that characters of the embryo which depend more or less directly upon the characters of the seed in which the embryo is produced should show matroclinous inheritance.

MATERIAL AND METHODS

The purpose of the present work was to study the inheritance of certain cotyledonary characters in *Cucurbita Pepo*. Seeds of various pure lines of this species and of F_1 and F_2 progenies from crosses between them were available from the cultures of Professor Sinnott. Soaked seeds were germinated in an incubator until the hypocotyl appeared and were then planted in flats. When the first foliage leaf was about one centimeter broad the seedlings were harvested and preserved in alcohol. After the cotyledons had become bleached they were detached and placed between thin glass plates which were inserted in the slide-holder of a projection lantern. The outlines and venation of the cotyledons were now projected and traced on drawing paper at three times their actual size. Certain measurements were taken from the cotyledons themselves and others from these projected drawings. In the pure lines and F_1, ten seedlings of each were studied, but at least twenty for each F_2 pedigree. For size measurements and shape

TABLE 1

Inheritance of cotyledonary shape index (length/width)

PURE LINES	MEAN	COEF. VAR.
C	1.35± .017	5.7± .87%
FSC	1.59± .014	4.1± .62
M	1.41± .024	8.1±1.10
MAR	1.78± .032	8.3±1.13
P	1.66± .020	5.6± .85
5	1.58± .024	6.9±1.05
10	1.49± .015	5.3± .81
22	1.21± .017	6.6±1.01
46	1.26± .012	4.2± .64
103	1.57± .013	3.8± .58
125	1.50± .026	8.0±1.22
391	1.25± .019	7.1±1.08
438	1.35± .024	8.1±1.10
741	1.46± .018	5.6± .85
BOT	1.70± .033	8.8±1.19
F_1 and F_2 Pedigrees		
F_1 103 x MAR	1.47± .013	4.1± .62
F_2 103 x MAR	1.62± .012	6.1± .52
F_1 125 x 22	1.45± .017	5.3± .81
F_2 125 x 22	1.47± .074	4.6± .39
F_1 M x C	1.51± .014	4.3± .54
F_2 M x C	1.50± .011	5.2± .53
F_1 Progenies		
103 x 22	1.66± .018	5.3± .81
22 x 103	1.39± .014	4.7± .72
438 x 5	1.36± .016	5.4± .82
5 x 438	1.45± .019	6.4± .98
103 x C	1.43± .017	5.3± .81
C x 103	1.43± .023	7.4±1.13
10 x 391	1.47± .009	2.7± .41
391 x 438	1.34± .012	3.9± .59
46 x 438	1.36± .014	4.8± .73
391 x FSC	1.36± .015	5.1± .78
M x FSC	1.41± .017	5.6± .85
C x P	1.53± .013	3.8± .58
P x 103	1.64± .012	3.2± .49
741 x P	1.43± .009	2.8± .42
5 x P	1.57± .013	3.7± .56
F_2 Progenies		
BOT x 103	1.66± .013	5.0± .47
103 x M	1.57± .019	8.4± .85
BOT x 10	1.56± .013	7.1± .59
BOT x 22	1.51± .013	7.4± .61
BOT x 46	1.56± .012	6.5± .56
BOT x 125	1.52± .017	6.8± .74

indices the two cotyledons from a seedling were averaged but for vein characters only one was used. Seed measurements (length and width) were also made on ten typical seeds from a plant. For cotyledons, the length and width of the blade were determined, as well as the maximum width of the two main vein islets, the distance between the points of origin of the first two branches of the midrib, and the angle between these branches. In addition to these quantitative characters certain qualitative differences were studied.

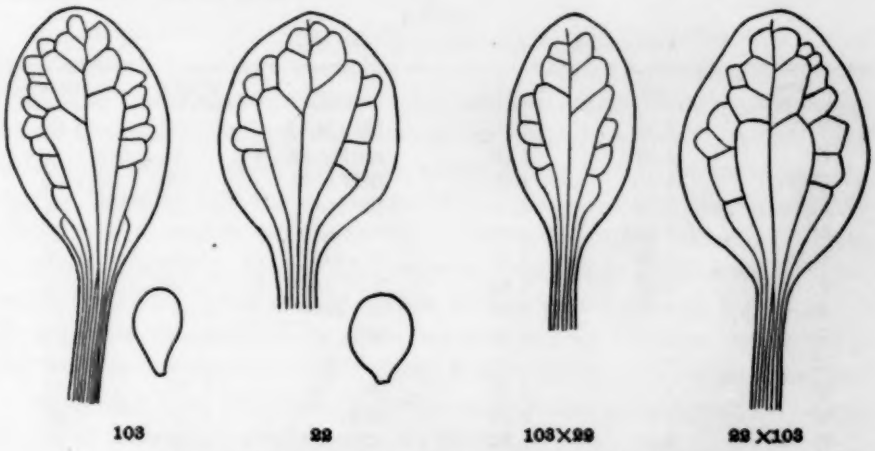

Fig. 1. At left, cotyledons of pure lines 103 and 22, with outlines of seeds of these lines, showing relation of seed shape to cotyledon shape. At right, cotyledons of the two reciprocal crosses between these lines, showing marked matrocliny in cotyledon shape inheritance.

Results

Size of cotyledons. This character is complicated by the marked influence of environmental conditions as well as by heterosis. The results of the present study, however, confirm the conclusions of previous workers that cotyledonary size is controlled in large part by the size of the seed in which the embryo is produced, and is thus matroclinous in its inheritance.

Shape of cotyledons. Table 1 presents data as to the mean and coefficient of variability for cotyledonary shape index (length of blade divided by width) in the pure lines and the various F_1 and F_2 progenies from crosses between them. The first group includes the pure lines, and marked differences in cotyledonary shape are evident among them. In the second group are three F_1 progenies with their corresponding F_2 offspring. The third group contains F_1 pedigrees from which no F_2 had been grown. In the fourth group are a number of F_2 pedigrees for which the F_1 was not available.

An examination of this table discloses a number of general facts with regard to shape inheritance. First, the mean index of an F_1 is in most cases much closer to that of its seed parent than to that of its pollen parent. Second, the variability of the F_2 generations is not strikingly higher than that of the F_1 and on the average is about the same as that of the pure lines. Third, the mean of the F_2 bears no necessary relation to that of the F_1 and is usually intermediate between the means of the two pure lines which were crossed.

TABLE 2

Comparison of shape indices of seeds and cotyledons

PURE LINES	SEED SHAPE INDEX	COTYLEDON SHAPE INDEX	CROSSES	F_1 SEED SHAPE INDEX	F_2 COTYLEDON SHAPE INDEX
BOT	1.75	1.70	103 x MAR	1.71	1.62
C	1.48	1.35	MAR x 103	1.77	1.71
CRK	1.80	1.54	BOT x 103	1.77	1.66
FLIW	1.75	1.68	103 x BOT	1.70	1.41
M	1.63	1.41	BOT x 10	1.76	1.56
MAR	1.75	1.78	10 x BOT	1.76	1.56
9	1.62	1.49	BOT x 46	1.68	1.56
10	1.70	1.49	46 x BOT	1.62	1.35
13	1.48	1.22	103 x M	1.62	1.57
22	1.32	1.21	125 x 22	1.74	1.47
43	1.68	1.51	391 x 741	1.54	1.38
46	1.67	1.26	M x C	1.57	1.50
90	1.60	1.50	BOT x 22	1.58	1.51
103	1.67	1.57	BOT x 43	1.71	1.42
105	1.53	1.54	BOT x 543	1.69	1.40
125	1.84	1.50	BOT x C	1.49	1.49
391	1.60	1.25	BOT x CRK	1.75	1.66
543	1.51	1.30	BOT x FLIW	1.93	1.74
741	1.46	1.46	9 x BOT	1.64	1.34

These facts can be readily explained if it is true that seed shape (a maternal character) directly determines cotyledon shape. The resemblance of the F_1 cotyledons to those of their female parents would thus be due to the fact that both were developed in seeds of the same shape. Neither segregation nor increase in variability would be expected in the cotyledons of the F_2 since these are all grown in F_1 seeds, which are essentially uniform in shape. Finally, there would be no necessary relation between the mean of the F_1 and the mean of the F_2, since the former would resemble the maternal pure line and the latter would be determined by the seed shape of the F_1 plants, which might be quite different from that of either parent.

To determine whether any direct relation exists between seed shape and cotyledon shape, the average shape indices for seeds and for the coty-

ledons of seedlings grown from these seeds were compared. The results in various pure lines and in hybrids between them are presented in Table 2. Although the seed index is higher than its corresponding cotyledonary index, the two indices tend to vary together. The coefficient of correlation between seed shape index and cotyledon shape index in the pure lines is found to be $+.52 \pm .036$, and between F_1 seeds and F_2 cotyledons, $+.64 \pm .083$. These facts indicate that seed shape does determine cotyledon shape to a considerable degree.

Although cotyledon shape seems thus to be influenced by seed shape and therefore to exhibit a certain degree of maternal inheritance, matrocliny is by no means complete. It is evident from Table 1 that certain pure lines behave differently from others in their effect on the F_1. In the cross of line 438 pollinated by line 5, for example, the F_1 cotyledons closely resemble those of 438, but in the reciprocal cross, 5×438, they are intermediate in character. Similarly, 103×22 resembles 103 whereas 22×103 is intermediate (fig. 1). In these crosses, lines 438 and 103 seem to have some effect on cotyledon shape when used as pollen parents but C and 5 do not. That this relationship does not always hold, however, is shown by the reciprocal crosses involving C and 103, in which the F_1 is intermediate in both cases. Line 438 seems to exert a considerable influence on cotyledon shape wherever it is used as a pollen parent.

Further evidence that there is a certain degree of normal biparental inheritance in cotyledonary shape is shown by the fact that the variability of the F_2 populations, while not at all high, is substantially higher than that of the F_1, the average of the former being 6.3% and of the latter 4.6%. To be sure, the average variability of the pure lines is fully as high as that of the F_2, but this is probably due to the lack of vigor which characterizes most pure lines and which results in the production of a good many small and defective seedlings, the presence of which in a population increases its variability.

We may conclude, therefore, that there is some indication of segregation here and that cotyledon shape, although markedly matroclinous in its inheritance, is not wholly so.

Vein characters. Between certain of the lines there are observable a number of slight but definite differences in cotyledonary vein pattern. The ratio of the width of the two main lateral islets to that of the cotyledonary blade, the distance apart in origin of the two main lateral veins arising from the midrib, and the angles which these make with the midrib were studied in certain pedigrees. In some crosses the vein pattern of the maternal parent would appear in the F_1 and in others that of the pollen parent.

Although critical evidence from reciprocal crosses was unfortunately not available in pedigrees where the greatest pattern differences occurred, it seems unlikely that these traits would show any evidence of matrocliny. This conclusion is strengthened by the fact that for these three characters the variability of the F_2 is consistently though not always significantly higher than that of the F_1.

Other traits. In line 43, out of 95 seedlings studied, 52 showed a tendency toward the fusion of the two cotyledons, either partial or complete. Only one cross involving line 43 was studied and here it happened to be used as the pollen parent. A considerable number of cases of fusion were observed in the F_1 and F_2, suggesting that this trait is inherited and can be transmitted through the pollen.

Certain differences in cotyledonary surface were also observed among the pure lines. A roughened or pebbly surface, caused by a swelling of the tissue between the veins, characterizes line 103. A lace-like pattern, due to the poor development of chlorophyll just above the veins, is found in line C. Both these traits behave as almost complete dominants, whether they enter a cross from the male or the female parent, and appear in a considerable portion of the F_2, although their segregation there is not sharp.

SUMMARY

The inheritance of various cotyledonary characters was studied in crosses between pure lines of *Cucurbita Pepo*.

Size of cotyledons is markedly influenced by seed size and thus tends to show a high degree of matrocliny.

Cotyledonary shape (ratio of length to width) is also determined to some degree by the seed parent through the influence of seed shape upon the developing embryo, but the pollen parent exerts a considerable effect in many cases and there is evidence here of a certain amount of normal biparental inheritance.

Characters of vein pattern and cotyledonary surface seem not to be maternally determined but to display ordinary inheritance.

The character of the cotyledons in this species is thus the result of a balance between the growth tendencies implanted in the embryo by its own genetic constitution, and the limitations imposed by the character of the seed in which this growth must take place.

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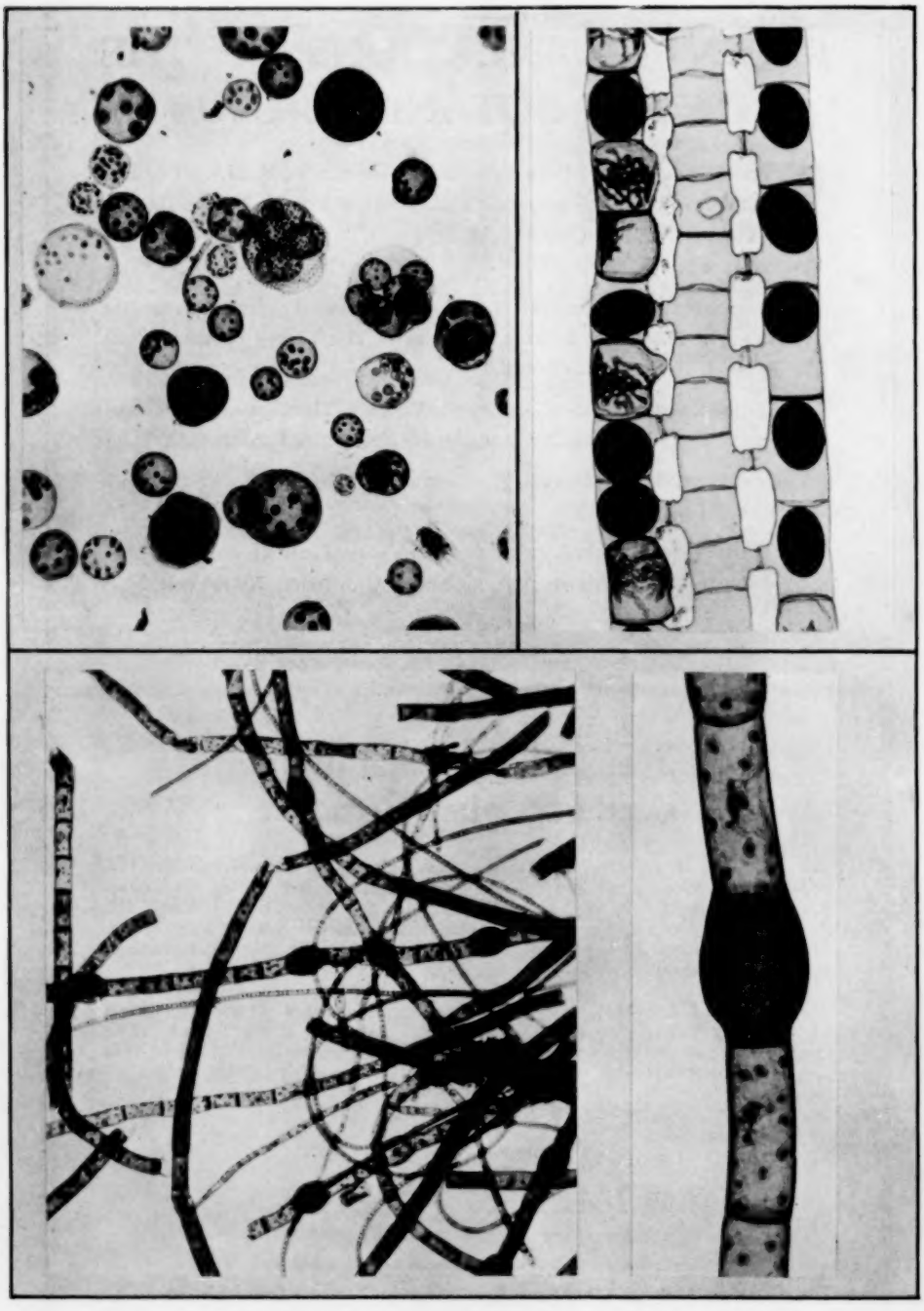

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